

contains an aqueous cytosol and a variety of organelles such as mitochondria and the Golgi apparatus; (4) each organelle has an internal structure (description and further levels varying by organelle). An example of functional decomposition is the discovery via physiological investigation that the overall function of pumping blood includes multiple component operations of contraction and relaxation (at different times in different chambers) and of opening and closing (of valves). The parentheticals indicate that it is generally difficult to specify operations without some indication of the parts involved. It is useful to have a separate notion of functional decomposition, though, because progress in identifying operations often can proceed when there is minimal knowledge of some or all of the parts involved. For example, biochemists in the early twentieth century decomposed the overall function of cellular respiration into numerous biochemical reactions (operations) while, structurally, they had basic knowledge of the substrates and products (passive parts) but little more than invented names for the enzymes (active parts) that were assumed to catalyze the reactions.

Ultimately, the full characterization of a mechanism requires mapping the operations into which the overall function of the mechanism is decomposed onto the parts into which the structure is decomposed. I use the term *localization* for such mappings and discuss them further below. Uncovering the organization of the parts and operations at a given level – not merely identifying them – is also crucial. Such a combined perspective is often required to understand fully how the mechanism generates its behavior, because frequently the spatial layout of the parts enables or facilitates the temporal organization of their operations. As a practical matter, moreover, structure and function frequently provide critical insights into the other. Learning the structural character of a part can provide insight into how it carries out its operation. Understanding the operation that is being performed often provides clues as to what sort of part is responsible. As we will see, many of the major contributions of modern cell biology to understanding the mechanisms responsible for the phenomena exhibited in living cells involved the ability to relate various organelles to the physiological operations they perform and, at a lower level, certain components of the organelles with particular biochemical operations.

Organization and Orchestration

A point just mentioned – that it is important to determine how parts and operations are organized – deserves elaboration. A mechanism is typically not just a collection of independent parts, each carrying out its operation in isolation. Rather, parts and operations are generally integrated into a cohesive,